

**Movement and Habitat Selection of Adult Largemouth Bass Associated
with Winter Drawdown in the Pend Oreille River, Idaho**

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Abstract

This paper characterizes movement and habitat selection of largemouth bass Micropterus salmoides associated with winter drawdown, and loss of backwater habitat in the 3,887 ha impounded section of the Pend Oreille River, Idaho. Twenty adult largemouth bass (> 300 mm total length) were captured in a 30-km section of reservoir, surgically implanted with radio transmitters, and monitored biweekly from September 1999 to June 2000. Habitats available to largemouth bass under drawdown conditions were separated into seven categories based on water depth, velocity, presence of cover and orientation to the main river channel, and quantified using Geographic Information System (GIS). In the fall, largemouth bass exhibited a shift from backwater habitat to shoreline areas along the main river channel in response to lowering water levels, however movement into over-wintering areas did not occur until early November, when drawdown was near completion and water temperatures were below 10 ° C. Two primary over-wintering areas (combined area 102.1 ha) contained 95 % of the largemouth bass monitored (n=19) from November to mid-March. Some fish traveled up to 16 km to winter in this area. Over-wintering areas were protected from main river currents, but were located outside of traditional backwater habitat, possibly to avoid cooler water temperatures in the back water habitat. Aquatic vegetation in 1-3 m of depth was associated with 90.2 % of the winter locations of largemouth bass, and was the most selected winter habitat. Our analysis suggests that largemouth bass were selecting not only specific habitat characteristics, but also a specific geographic area.

Introduction

Lowering water levels during winter is common in many dammed large river complexes to maximize power generation and prevent flooding. The implications of these practices, however, can adversely affect off-channel areas that function as essential over-wintering habitat for many riverine fishes (Greenbank 1956; Pitlo 1992; Sheehan et al. 1990; Raibley et al. 1997). Winter drawdowns can directly influence winter habitat through de-watering and exposure of off-channel areas, forcing fish to seek alternative winter habitat or over-winter in less suitable conditions associated with the main river channel (Pitlo 1992). Indirect effects of winter drawdown are related to a reduction in water depth. Shallow backwaters are especially susceptible to oxygen depletion during periods of extensive snow and ice cover (Mathias and Barica 1980), and can often reach water temperatures near 0 ° C. Large or untimely water level fluctuations during the winter may also trap fish in backwaters, and can lead to fish kills (Greenbank 1956). Winter survival of centrarchid fishes in riverine environments has been linked to the accessibility and quality of backwater habitat (Greenbank 1956; Carlson 1992; Pitlo 1992; Hatch 1991).

The Pend Oreille River, Idaho has been subjected to winter drawdown conditions that severally limit access to side channels and backwaters previously identified to be important winter habitat for centrarchid fishes. Recent concern over improving the warmwater sport fishery in the river has prompted a series of investigations designed to better understand the relation between drawdown conditions and over-winter survival. As a part of this research, a radio telemetry

study was conducted to evaluate the winter behavior and habitat selection of fish in response to winter drawdown conditions in the reservoir. Knowledge of winter habitat needs is important because it can be used to influence decisions concerning water level management and improving the warmwater sport fishery.

The specific objectives of this study were to:

1. Describe movement and habitat selection of largemouth bass associated with winter drawdown conditions in the Pend Oreille River, Idaho; and
2. Evaluate the role of winter water elevations in the selection of over-wintering habitat by largemouth bass.

Study Area

The Pend Oreille River begins at the outlet of Lake Pend Oreille, which is located in the northern Idaho at an elevation of 628.5 m (2061 ft) above mean sea level (Figure 1). Our study area was the upper portion of the river, extending from Albeni Falls Dam upstream 44.25 km to the U.S. Highway 95 bridge near the City of Sandpoint, Idaho. This section of river is operated as a run-of-the-river reservoir, with flows ranging seasonally from 617 to 2,044 m³ (11,200-73,000 cfs). At full pool, the surface area is approximately 3,887 ha, the maximum depth is 48.5 m, and the average depth is 7.1 m (Dupont 1994). About 161 km of the shoreline, including sloughs and islands, has a gentle to moderate slope consisting mostly of fine sediments (< 4 mm), while about 16 km of shoreline is rocky, consisting of rip-rap (DuPont 1994). Aquatic macrophytes, mainly *Potamogeton spp.* and *Myriophyllum sibiricum* are abundant along the shoreline in many areas (Wagner 2000).

Six major backwaters occur in this section of the Pend Oreille River: Riley Creek Slough (Rkm 18.2), Hoodoo Creek Slough (Rkm 19.0), Tanner Creek Slough (Rkm 21.7), Cocolalla Slough (Rkm 23.2), Morton Slough (Rkm 25.4), and Gypsy Bay (Rkm 31.6; Figure 1). These areas are isolated from main river currents, have relatively shallow water depths (from 2 to 3.8 m), and contain heavy growths of aquatic macrophytes. Prevalent warmwater fishes, including pumpkinseed Lepomis gibbosus, largemouth bass, black crappie Pomoxis nigromaculatus, and yellow perch Perca flavescens, are typically found in high abundance in these adjacent areas (Dupont 1994). These areas were suspected to provide suitable winter habitat if winter water levels were increased.

Waters upstream of Albeni Falls Dam are evacuated annually from late fall to early spring for flood control and winter electrical generation (Dice 1983). During this study, drawdown began on 19 September and continued through 3 November 1999, at a mean rate of about 4.5 cm/day (Figure 2). Water levels were maintained at a target elevation of 625.8 m (2052 ft) from November to May, approximately 2.9 m lower than full pool elevation 628.5 m (2061 ft). Under this drawdown regime, Hoodoo Creek Slough, Gypsy Bay, and Riley Creek Slough were completely dewatered, and of the remaining three backwaters, only Morton Slough maintained water depths near 1.5 m. Spring refill began 5 May and reached full pool on 15 June 2000, at a mean rate of about 5.3 cm/day.

Methods

Data Collection

Winter movement patterns and habitat use of largemouth bass were determined throughout the study area using radio telemetry. Twenty adult largemouth bass were captured from 29 August through 19 October 1999 using boat electrofishing and angling (Table 1). Captured fish were anesthetized (MS-222), measured for total length (mm) and weight (g), and surgically implanted with a 17 by 40 mm (17 g dry weight) radio transmitter (model 5902, Advanced Telemetry Systems, Inc., Isanti, Minnesota) following similar techniques described by Ross and Kliner (1982), and Hart and Summerfelt (1975). Each transmitter was equipped with a braided wire antenna and coated with clear waterproof epoxy resin. Transmitters contained 3.0 V lithium batteries with a 300-d capacity, and each operated on a unique frequency between 151-152 MHz. Following surgery, largemouth bass were tagged with a serially numbered Floy[™] tag for external identification, and returned to a holding tank until recovery, usually 10-20 minutes. Fish were released at the site of capture.

Each fish was contacted at least every 2 weeks through June of 2000, following a 7-day acclimation period (Guy et al. 1992). Radio-tagged fish were located using a boat equipped with a fixed signal receiver (model FM 1470, Advanced Telemetry System, Inc., Isanti, Minnesota), and a four-element 1.2 m yagi antenna. A hand-held directional antenna was used once in the general vicinity of a fish to determine its definitive location (< 2 m). Fish locations were recorded in Universal Transverse Mercator (UTM) coordinates using a global positing unit (GPS)

with an external antenna (Trimble Geoexplorer II). Date, time of day, water temperature ($^{\circ}\text{C}$), total depth (m), velocity (cm/sec), dissolved oxygen (DO; mg/L), turbidity (NTU), distance to nearest shore and cover type were also recorded at each contact point. Location files along with habitat parameters were downloaded to a computer, differentially corrected, and imported into ArcView v.3.2 (Environmental Systems Research Institute, ESRI) for analysis.

Habitats available to largemouth bass under winter drawdown conditions were determined from maps describing water depth, velocity, and presence or absence of aquatic macrophytes. Maps of water velocity and aquatic macrophytes were produced from field measurements collected during December 1999 and January 2000, while water depth was determined using a bathymetric contour map obtained from United States Geologic Survey (USGS 1996). All data collected on habitat variables were imported into ArcInfo v.7.2.1. and ArcView v.3.2. (ESRI) for spatial analysis.

Mean daily water elevations were obtained from the U.S. Army Corps of Engineers through readings at the Hope recording station on Lake Pend Oreille. Water temperature was recorded hourly at two permanent stations (main river channel and backwater; Figure 1) using three temperature loggers (model RIM 200, Ryan Instruments, Inc., Redmond, Washington) suspended at bottom, mid-depth, and surface positions.

Data Analysis

Minimum winter migration distance was calculated for each radio tagged fish as the linear distance from the location of initial capture to that of its preferred over-wintering area. Distance traveled was calculated using the Animal Movement extension in ArcView (ESRI 1997). This is a minimum distance of movement because fish were not monitored continuously.

Areas that remained wetted following the completion of winter drawdown and maintained water velocity < 1 cm/sec were deemed available to over-wintering largemouth bass as recommended by Winter and Ross (1982). Observations of use and availability were divided into seven habitat categories based on water depth, presence or absence of aquatic macrophytes, and orientation to the main river channel. These categories included: vegetated-shallow depth (0 - 1 m), open water-shallow depth, vegetated-medium depth (1 - 3 m), open water-medium depth, vegetated-deep depth (3 - 5 m), open water-deep depth, and backwaters (open water and vegetated, 0 - 1.5 m).

To determine the availability of each habitat category within the study area, a composite map was generated by logically overlaying the three habitat maps (water depth, velocity, and vegetation) and a shoreline reference map using the map-calculator command in ArcView v.3.2. (ESRI). Largemouth bass use of each habitat category was evaluated by overlaying a map of fish locations on the composite map delineating each habitat category. For each fish, the number of observations within each habitat category was then enumerated, and a chi-square test of independence ($\alpha = 0.05$) was used to test whether all fish were selecting similar habitat types.

Compositional analysis (Aebischer et al. 1993) was used to test whether largemouth bass selected over-wintering habitat categories in proportion to their availability. For this analysis, the number of observations within each habitat category was compared with the expected number given a random distribution of observations in each habitat category (H_0 : use = availability). If a significant difference were detected, a pairwise t-test was used to rank the habitat types by relative use. All calculations were performed using Resource Selection v.1 (Leban 1999), and only contacts made during the period between November and mid-March were used to determine winter habitat selection.

Results

Movement and Behavior

We radio tagged 20 adult largemouth bass within a 30-km section of the Pend Oreille River, in both backwater and main river habitats (Figure 3). A total of 381 locations were obtained from 19 largemouth bass from 2 October 1999 to 2 June 2000 (Table 1). The mean number of observations was 20/fish (range 14 - 26), and fish were tracked over an average of 246 d (range 170 - 276). No signals from one largemouth bass (no. 073) were ever received following release, and we assumed the radio tag was defective. We observed no emigration of fish outside the study area over the duration of this study.

Largemouth bass exhibited a shift from backwater habitat to shoreline areas along the main river channel coinciding with drawdown. Early attempts to capture largemouth bass were difficult, because larger fish appeared to be distributed over the study area. Consequently, only 10 largemouth bass were radio tagged prior to the initial drawdown in September. Of these, five were initially captured in backwater habitat. Following the onset of drawdown, these fish moved into deeper shoreline areas along the main river channel, but remained in the general vicinity of their original capture location. Further collections of largemouth bass for radio tagging also reflect this shift away from off-channel areas, as only three of the remaining 10 largemouth bass were captured in backwater habitat. By mid-October, when tagging was completed, all experimental fish were located outside of adjacent backwaters, but remained distributed throughout the study area. Movement towards over-wintering

areas and away from initial capture locations began in late-October as water temperatures in the main river channel decreased below 10 ° C, and winter drawdown was near completion.

On 4 November, 18 of 19 (95 %) largemouth bass were located in one of two primary wintering areas (PWA; Figure 4). The upper PWA (49.3 ha) was located along the shoreline immediately down-river of Gypsy Bay, while the lower PWA (52.9 ha) was located from the mouth of Morton Slough down-river to Tanner Creek Slough (Figure 4). Both areas were characterized as having zero water velocity, a gentle sloping bottom with a mean water column depth of 2 m and dense aquatic macrophyte growth. Of the 18 largemouth bass that wintered in these areas, all but one remained until early spring. In mid-January, one fish (no. 053) moved out of the upper PWA, and was located up-river 4.8 km along the south shoreline, where it remained until spring refill. The only experimental fish (no. 135) that over-wintered outside the PWA complex was located along the south shoreline at Rkm 13.5, where it remained for the duration of winter. Habitat characteristics where this fish over-wintered were similar to those found in the PWA.

Some fish traveled extensive distances to over-winter in the PWA (Table 1). One fish (no. 294) traveled from its initial capture site at the mouth of Priest River (Rkm 8.0), up-river at least 16 km. Two other fish (nos. 035 and 153) moved at least 10 km down-river, and traversed the main river channel before entering the lower PWA. Those fish initially captured near Morton and Cocolalla sloughs generally traveled under 2 km (Table 1). Although we were unable to follow the daily

movement of largemouth bass migrating to over-wintering areas, it appeared that most fish moved along the shoreline in the lowest water velocity.

Two general trends of largemouth movement occurred once in the over-wintering areas. One group ($n = 9$) remained relatively sedentary, especially once water temperature decreased below 6°C in December. These fish were repeatedly contacted in the lower PWA near the mouth of Morton Slough within an area less than 15 ha. Fish in the other group ($n = 9$) remained more active. For example, over a 3-day period in early January, at water temperatures approximately 3°C , fish no. 035 moved from the mouth of Morton Slough (lower PWA) up-river a minimum of 3.9 km to shoreline outside of Gypsy Bay (upper PWA). During this same 3-day period, another fish (no. 114) moved 5.1 km from outside of Morton Slough down-river to the mouth of Tanner Creek Slough. This pattern of movement between areas within PWA was observed throughout the winter, and did not appear to be affected by water temperature. However, movement was confined to areas protected from water velocity.

Temperature and dissolved oxygen (DO) profiles within the PWA indicated stratification did not occur during winter 1999-2000, as temperatures only differed from the top to the bottom by 0.1 to 0.5°C and dissolved oxygen consistently remained higher than 12 mg/l . By mid-December ice formed in backwaters and along shoreline areas of the upper and lower PWA, and remained until early March. Largemouth bass were frequently contacted under the ice, but remained in areas outside of defined backwaters. We found no indication of hypoxic conditions as a

result of ice cover along the main river or backwater habitat (measurements of DO taken under the ice ranged from 8.5 to 14.5 mg/l).

Movement away from the PWA complex began in mid-March when water temperatures in existing backwaters increased beyond those in the main river (Figure 2). On 13 March, we discovered three largemouth bass (nos. 193, 674, and 733) had moved from the lower PWA into Morton Slough. By 25 March, all the experimental fish that over-wintered in the upper and lower PWA were located in adjacent backwaters that remained accessible following drawdown. The majority of these fish ($n = 15$) were located in Morton Slough, however fish no. 773 was located in Cocolalla Slough, and fish no. 114 was located in Tanner Creek Slough. Fish no. 135 that wintered down-river from the PWA was also found in a shallow inlet near its over-wintering location. From March to April, mean water temperatures in backwaters increased from 7.5 to 15 °C, and remained about 3 °C warmer than the main river (Figure 5). During this period, all fish were close to shore in waters < 1 m in depth, and in no detectable cover. All experimental fish that moved into backwaters in March remained in these areas until spring refill in May.

During spring refill, tagged largemouth bass redistributed throughout the study area, but were typically located in reinundated backwaters. Of the 12 fish located following the completion of spring refill in June, nine had returned to areas where they were originally captured. For instance, largemouth bass no. 294 returned 16 km down-river to within a few meters of its original capture site. Similarly, fish no. 153 returned to its original capture site approximately 10 km up-river. The majority of fish initially captured near Morton Slough remained in the general area,

however, two largemouth bass (nos. 095 and 773) moved beyond the main river boundary via connecting culvert into the principal water body of Cocolalla Slough.

Winter Habitat Selection

A drawdown of 2.9 m in the Pend Oreille River in winter 1999 reduced the total surface areas by about 11.3 %, and exposed approximately 423 ha of shoreline. Under these conditions, the most frequently occurring habitat types available to largemouth bass were (1) open water-medium depth (1 – 3 m; 52.9 % of the available area), and (2) vegetated-medium depth (23.5 % of the available area; Table 2). Areas defined as vegetated-deep depth (3 - 5 m) accounted for the least amount of available habitat (1.4 %).

Largemouth bass selected proportionally similar habitat types ($\chi^2 = 53.54$, $P = 0.49$) during the winter, and were therefore pooled to determine habitat selection. Of the 225 fish contacts made from November to mid-March, 202 (90.2 %) were located in habitats defined as vegetated-medium depth (1 - 3 m), which was only 23.5 % of that available. In contrast, only 17 (7.6 %) contacts were made in open water-medium depth, despite this habitat accounted for 52.9 % of available habitat. Observations in areas defined as open water-shallow depth (0 - 1 m) and vegetated-shallow depth each accounted for 1 % of that used. Fish were not observed wintering in vegetated-deep depth (3 - 5 m), open water-deep depth (3 - 5 m) or backwaters, or outside areas defined as available (*i.e.* areas with water velocity > 1 m/sec).

Compositional analysis indicated that overall habitat use was clearly nonrandom ($\chi^2 = 128.9$; $P < 0.0001$). A pairwise comparison t-test indicated that

largemouth bass selected vegetated-medium depth habitat significantly higher than all other habitat types ($P < 0.0001$), and was therefore ranked 1 (i.e. most selected; Table 3). We found no significant difference between use of habitat types ranked 2 through 6, implying that these habitats are interchangeable, however open water-medium depth (ranked 2) received significantly higher use than backwater habitat (ranked 7).

Discussion

Results of this study clearly demonstrate the importance of specific wintering areas to largemouth bass in the Pend Oreille River. From the beginning of November to mid-March, 95 % of the largemouth bass monitored ($n = 19$) within a 30-km section of the reservoir were located in one of two small wintering areas (combined surface area 102.2 ha). These areas provided refuge from water velocity and maintained relatively stable and warmer water temperatures; both characteristics previously identified as suitable winter habitat (Sheehan et al. 1990; Pitlo 1992). However, primary over-wintering areas were located along the main river channel outside of existing backwaters. This is in contrast to previous studies that suggest off-channel areas typically provide suitable habitat and attract high densities of fish during the winter (Greenbank 1956; Sheehan et al. 1990; Pitlo 1992; Raibley et al. 1997). Possibly, largemouth bass over-winter along the shoreline of the Pend Oreille River because of the lack of suitable backwater habitat under drawdown conditions.

Largemouth bass were probably not attracted to existing backwaters because of shallow water depths and unfavorable thermal conditions created by lower water levels. A drawdown of 2.9 m reduced the total surface of the Pend Oreille River by

approximately 11 %, exposing about 423 ha of shoreline. Most this area consisted of shallow backwaters or sloughs located adjacent to the main river channel. Although backwaters not completely dewatered remained accessible to fish, only Morton Slough maintained water depths exceeding 1 m. Consequently, shallow backwaters cooled more rapidly in the fall, and remained an average 3 ° C cooler than the main river channel until early January (Figure 2). Largemouth bass have been shown to thermal regulate (Cherry et al. 1975; Crawshaw 1984; Cincotta and Struffer 1984), and will seek areas providing the warmest available water to over-winter (Coutant 1975; Ross and Winter 1982; Sheehan et al. 1990; Pitlo 1992; Raibley et al. 1997). Therefore, we believe warmer main channel areas with little to no water velocity probably served as thermal refuge from cooler backwaters, and provided alternative winter habitat under drawdown conditions.

The ability to find suitable winter habitat can be critical to the survival of largemouth bass in riverine environments at northern latitudes. For instance, Pitlo (1992) found that when low water levels denied access to suitable winter habitat in the upper Mississippi River, radio-tagged largemouth bass suffered higher winter mortality. Gent et al. (1995) also noted declines in largemouth bass populations in the Mississippi River following destruction of backwater habitat due to sedimentation. The fact that all radio tagged largemouth bass successfully over-wintered outside of adjacent backwaters in the Pend Oreille River suggests that essential habitat components were being met.

The high concentration of experimental fish, combined with the distance some fish traveled to reach preferred over-wintering areas may however reflect a general

lack of suitable winter habitat under drawdown conditions. We found that within preferred over-wintering areas, radio tagged largemouth bass selected habitats containing aquatic vegetation in waters 1-3 m in depth. Based on our analysis of habitat availability, these habitat characteristics were present in other areas within the reservoir, but were unoccupied by experimental fish. In fact, several fish by-passed these areas when migrating to preferred winter locations. Measurements of water temperature, DO, and velocity taken from these areas throughout the winter indicate little difference from the PWA. This suggests that fish may be orienting to certain characteristics of over-wintering habitat that were not obvious from our research.

One possible reason for the strong affinity of largemouth bass to the specific over-wintering areas may be related to the overall size of the areas. While we found that other reservoir sections also contain preferred habitat, primary over-wintering areas contained the largest continuous surface area of aquatic vegetation. Other areas of preferred habitat were smaller, with more sparsely distributed aquatic vegetation.

Another hypothesis to the apparent importance of these specific areas might be related to homing behavior. The ability of largemouth bass to return to particular over-wintering areas has been documented in previous studies (Carlson 1992; Pitlo 1992). While we are unable to determine whether largemouth bass return to the same wintering areas year after year, homing behavior and winter site fidelity may explain the strong allegiance to these particular locations.

Largemouth bass prefer habitats containing aquatic vegetation to open water. The strong association between largemouth bass and under water structure has been demonstrated (Johnson et al. 1988; Walters et al. 1991). Selection of aquatic

vegetation may be attributed to the lack of alternative shoreline cover (e.g. woody debris, boat docks) exposed following winter drawdown. Large beds of aquatic macrophytes, mainly *Potamogeton spp.* and *Myriophyllum sibiricum*, provided winter refuge throughout the winter. Increased habitat complexity has been shown to enhance over-winter survival of juvenile largemouth bass by providing shelter from predators (Miranda and Hubbard 1994), and may prevent fish from being washed down-stream (Carlson 1995).

Water temperature appeared to influence the movement of largemouth bass into and away from over-wintering areas. In the fall, largemouth bass exhibited a shift from backwater habitat into deeper shoreline areas coinciding with cooler water temperatures. Fish remained outside of shallow backwaters until early spring, when water temperatures warmed, and fish moved back into shoreline areas. Earlier studies have reported largemouth bass winter migrations that are characterized by fish shifting offshore during the winter and returning when water temperatures warm (Betsill et al. 1986; Woodward and Noble 1997). Access to warmer water temperatures in the spring may allow adult fish to begin spawning activity earlier, which may lead to a longer growth period, and ultimately improved survival of young-of the-year (Bowles 1985; Hatch 1991).

Although most radio-tagged largemouth bass did not leave the wintering areas, some fish continued to move within them. In contrast, largemouth bass were relatively sedentary during winter in other studies (Warden and Lorio 1975; Pitlo 1992), probably because decreased metabolic activity occurs at low temperatures (Johnson and Charlton 1960; Crawshaw 1984). The reason for sustained activity by

some fish is unclear. Largemouth bass have been shown to move under low water temperatures to avoid low DO levels (Sheehan et al. 1990; Railey et al. 1997; Gent et al. 1995). However, DO levels in both backwater and main river habitats remained high (> 8 mg/l) throughout the winter. Movement in response to predator-prey interactions is also unlikely, since feeding activity by largemouth bass is significantly reduced at water temperatures below 10°C (Crawshaw 1984). Continued winter mobility may represent a mobile segment that exists within some largemouth bass populations (Woodward and Noble 1997), although this behavior has been most commonly observed in intermediate size classes (250-320 mm), and not during the winter.

Management Implication

From a fisheries management perspective, the high concentration of largemouth bass over-wintering in relatively small areas outside of traditional backwater habitat, suggest winter drawdown practices are limiting winter habitat. Future efforts to minimize winter drawdown in the Pend Oreille River would benefit largemouth bass and other warmwater games fishes that require off-channel habitats to successfully over-winter. However, with increased need for power production in the Pacific Northwest, maintaining higher winter water levels may not be a political option. In light of this, alternative management options that enhance suitable winter habitat under winter drawdown conditions should be considered.

One possible way of enhancing suitable over-wintering habitat is increasing the overall depth of adjacent backwaters and littoral areas through mechanical

dredging. Results of our study indicate that largemouth bass were not attracted to existing backwaters because of shallow water depths and unfavorable thermal conditions created by low water levels. Increasing the depths of these areas would promote warmer minimum temperatures and enhanced water temperature stability; both factors benefiting over-wintering fishes. However, a large-scale dredging operation is probably economically impractical for rehabilitating entire backwater complexes. One possible solution might be to rehabilitate backwaters by temporally damming, and isolating them from the main river channel. These areas could be then dewatered, allowed to dry, excavated, and then reconnected with the main river.

On a smaller scale, deepwater refuge could be created in known over-wintering areas to improve winter habitat conditions. For example, Gent et al. (1995) found that radio tagged largemouth bass over-winter in channels excavated to provide fish habitat in Brown's Lake, a sediment-filled backwater of the Upper Mississippi River. Creation of deepwater refuge in a few select areas may be more cost-effective than large-scale dredging, and still effectively enhance winter habitat.

Management of aquatic macrophytes also should be considered when enhancing suitable winter habitat. Our results indicate that largemouth bass preferred to winter in areas containing aquatic macrophyte growth rather than in open water. Lowering water levels during the winter, and exposing vast amounts of shoreline has been shown to significantly reduce aquatic macrophyte densities along littoral areas (Wagner 2000). A further reduction in winter drawdown would limit the extent of vegetated areas, and may thereby limit suitable winter habitat.

This study was designed to evaluate the winter behavior and habitat selection of adult largemouth bass, with little emphasis on younger age classes. As a result, we cannot confidently comment on whether smaller individuals exhibit similar winter behavior. Suitable winter habitat is especially critical to age-0 largemouth bass, because they are most susceptible to winter related mortality (Hatch 1991; Sheehan et al. 1990). Copland and Noble (1994), who monitored the displacement of tagged age-0 and age-1 largemouth bass in a reservoir, found little migration tendencies of fish away from their release sites over a five month period, even during a short period of low water levels. Hence, younger largemouth bass may not response to receding water levels by moving into deeper water, which may lead to higher winter mortality. Because recruitment of largemouth bass in northern waters is strongly based on over-winter survival of age-0 fish (Bowles 1985; Rieman 1987; Hatch 1991), we suggest that further investigation on winter behavior and habitat selection of these individuals is needed.

Of the 19 radio tagged bass tracked throughout the winter, two were harvested by anglers the following spring. At least three other fish were caught by anglers and released. It is possible that the five radio-tagged largemouth bass not detected after April were harvested and not reported. Spring angling effort particularly in backwater areas has increased in the Pend Oreille River in recent years (Larry Miller, Idaho Department of Fish and Game, personal communication). This is largely attributed to relatively high catch rates of largemouth bass in Morton and Cocolalla sloughs, presumably from high concentrations of fish. Increased angling pressure in

areas that attract largemouth bass in the spring could have deleterious effects on the population and should be intensely monitored.

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Table 1. Summary of radio tagged largemouth bass in the Pend Oreille River, Idaho.

Fish code Number	Total Length (mm)	Weight (kg)	Study Dates ^a	Number of locations	Distance traveled ^a (km)
151.035	471	2.20	29 Aug 1999 - 16 Apr 2000	20	8.4
151.095	495	2.52	29 Aug 1999 - 2 Jun 2000	22	3.8
151.073	500	2.20	29 Aug 1999 - ^b	2	-
151.114	405	1.00	2 Sep 1999 - 31 May 2000	26	0.8
151.135	434	1.17	3 Sep 1999 - 31 May 2000	16	2.2
151.153	465	1.74	5 Sep 1999 - 2 Jun 2000	26	10.5
151.193	396	1.00	17 Sep 1999 - 16 Apr 2000 ^c	19	1.5
151.173	393	0.80	17 Sep 1999 - 29 Apr 2000	18	1.3
151.253	412	1.05	18 Sep 1999 - 29 Apr 2000	20	1.2
151.233	400	1.03	18 Sep 1999 - 31 May 2000	21	1.3
151.273	372	0.77	2 Oct 1999 - 31 May 2000	20	1.5
151.315	398	0.97	3 Oct 1999 - 29 Apr 2000	18	1.0
151.294	485	1.79	3 Oct 1999 - 31 May 2000	19	15.9
151.693	356	0.69	7 Oct 1999 - 31 May 2000	21	1.3
151.674	365	0.69	7 Oct 1999 - 25 Mar 2000 ^c	17	1.4
151.334	470	1.56	7 Oct 1999 - 31 May 2000	20	0.9
151.773	365	0.71	8 Oct 1999 - 2 Jun 2000	24	0.8
151.014	475	2.13	9 Oct 1999 - 2 Jun 2000	21	1.0
151.733	505	2.16	9 Oct 1999 - 31 May 2000	19	1.1
151.053	488	1.93	19 Oct 1999 - 13 Mar 2000	14	4.8

^a From implantation of transmitter to wintering area.

^b Signal was never received after release.

^c Fish were harvested by anglers.

Table 2. Relative abundances (%) of habitats available to tagged largemouth bass during the winter period of November through mid-March, and percentages of observations within each habitat.

Habitat type	Abbreviation	Habitat Availability	Habitat Use
Vegetated-shallow depth (0 - 1 m)	VSD	5.3	1.2
Open water-shallow depth (0 - 1 m)	OWSD	5.9	1.0
Vegetated-medium depth (1 - 3 m)	VMD	23.5	90.2
Open water-medium depth (1 - 3 m)	OWMD	52.9	7.6
Vegetated-deep depth (3 - 5 m)	VDD	1.4	0.0
Open water-deep depth (3 - 5 m)	OWDD	3.7	0.0
Backwater	BW	7.3	0.0

Table 3. A ranking matrix for tagged largemouth bass based on comparing the proportions of use and availability of each habitat type. Signs (+ or -) indicate selection for and against a given habitat; triple sign (+++ or ---) indicate significant deviation from random at $P < 0.05$. See Table 2. for habitat abbreviations.

Habitat type	Habitat type							Rank
	VSD	OWSD	VMD	OWMD	VDD	OWDD	BW	
VSD		-	---	-	-	+	+	3
OWSD	-		---	-	-	+	+	4
VMD	+++	+++		+++	+++	+++	+++	1
OWMD	-	-	---		-	-	+++	2
VDD	-	-	---	-		+	+	5
OWDD	-	-	---	-	-		-	6
BW	-	-	---	---	-	-		7

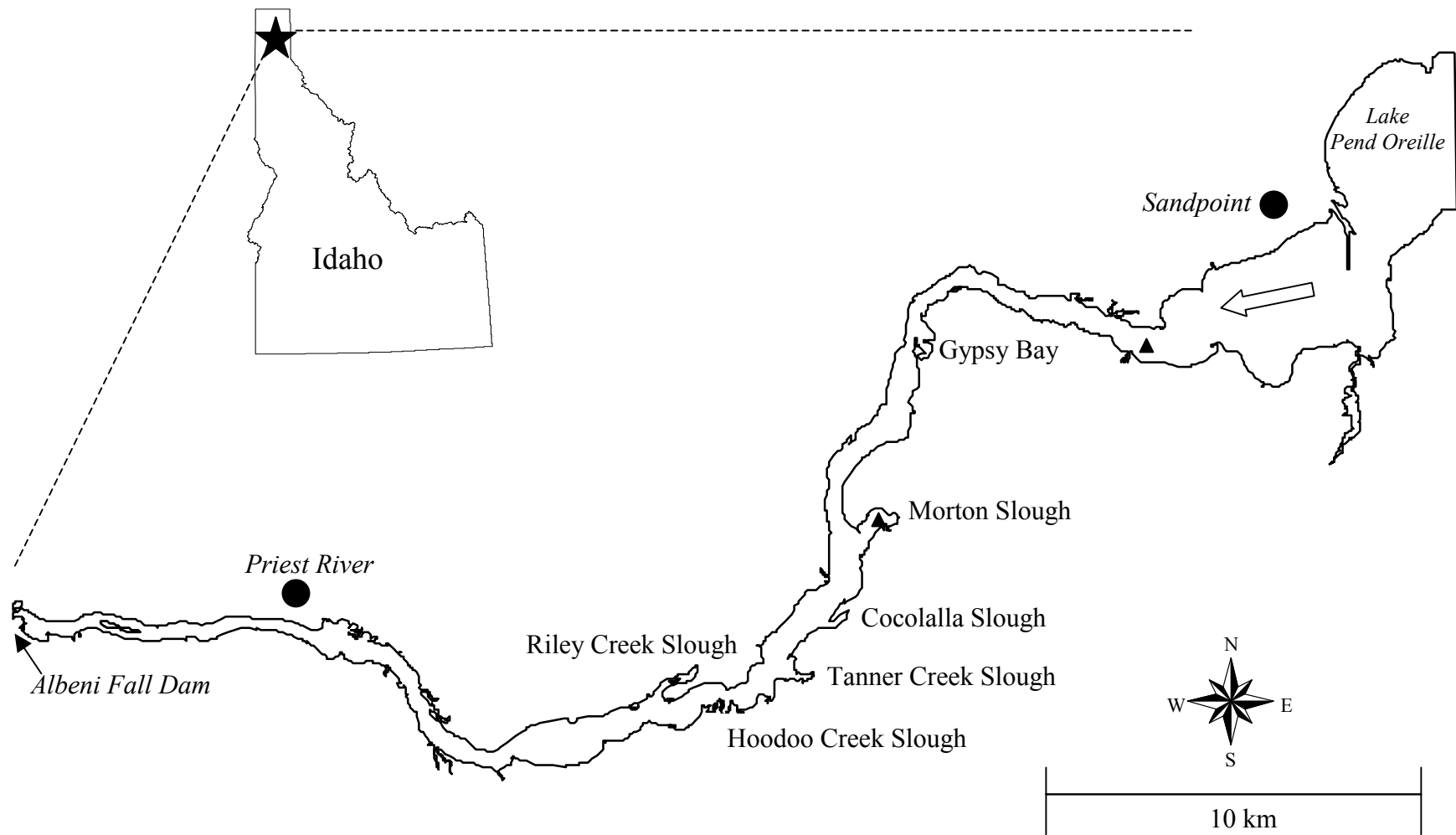


Figure 1. Study area map of the Pend Oreille River including the six primary backwater areas. Triangles (▲) show the locations of the 2 temperature recording stations.

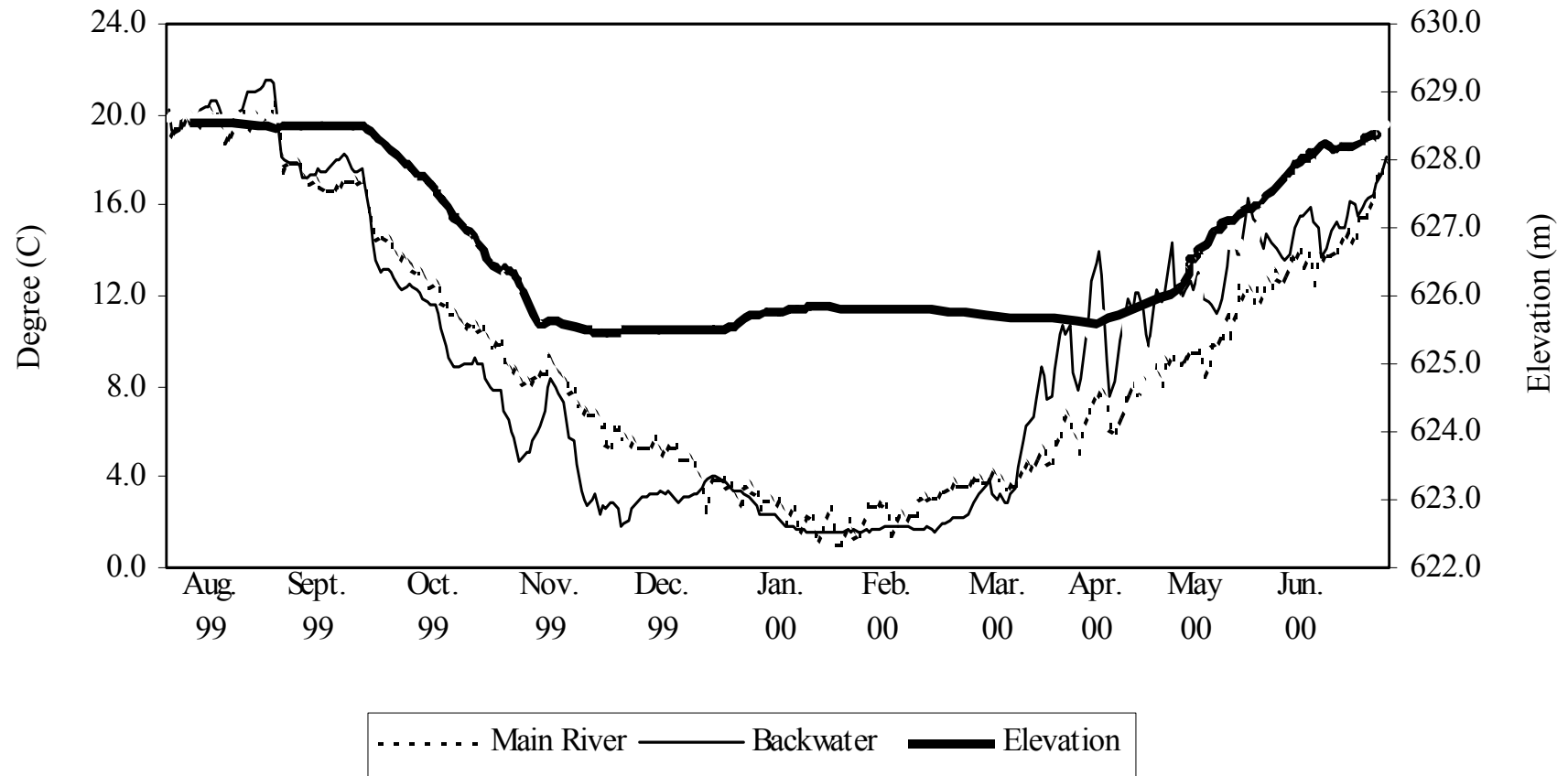


Figure 2. Mean daily water temperatures and water surface elevation from August 1999 to June 2000, in the Pend Oreille River, Idaho.

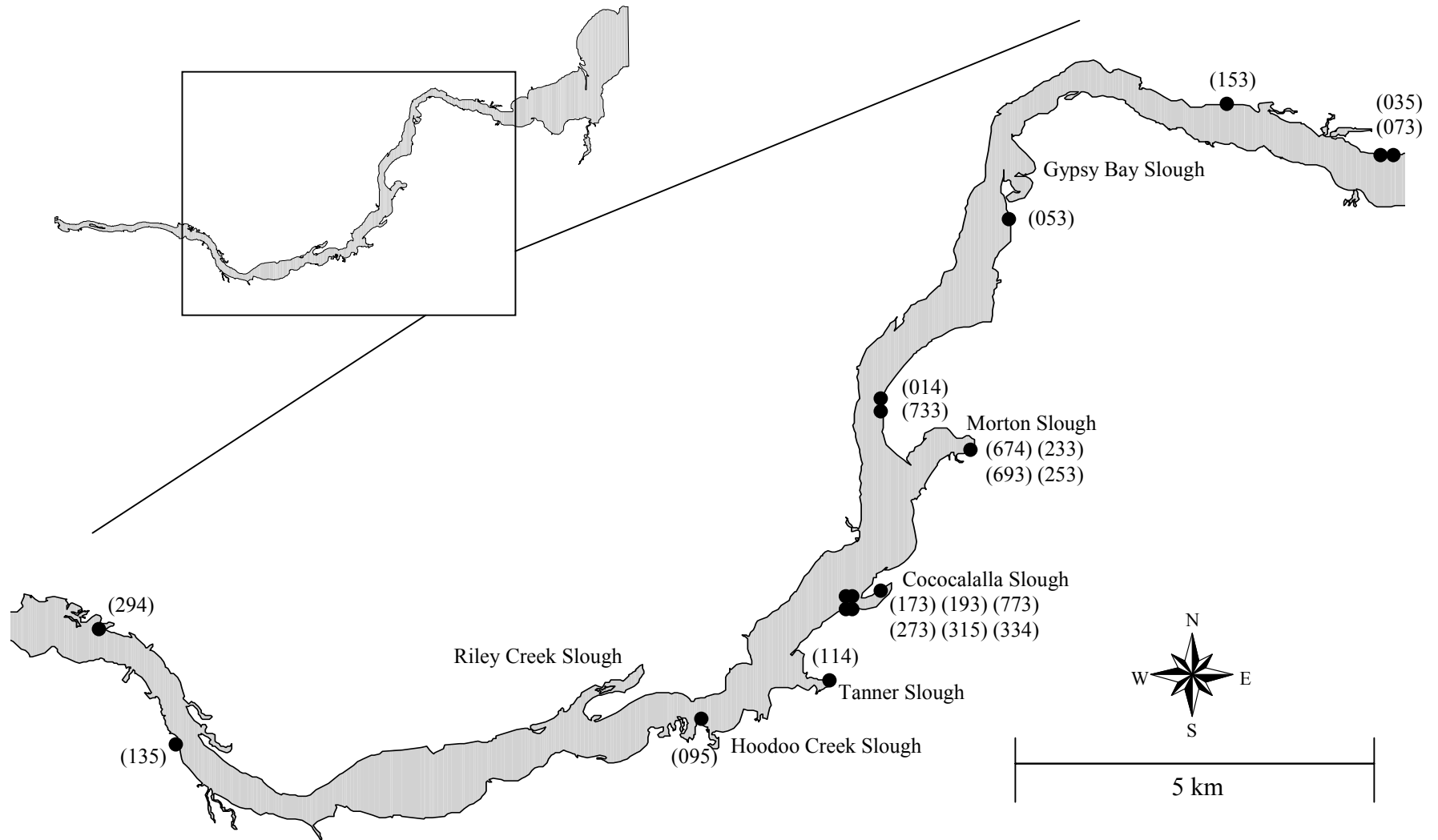


Figure 3. Initial capture locations of 20 radio tagged largemouth bass collected from August 29 to October 19, 1999 in the Pend Oreille River, Idaho. Parentheses contain codes of individual fish.

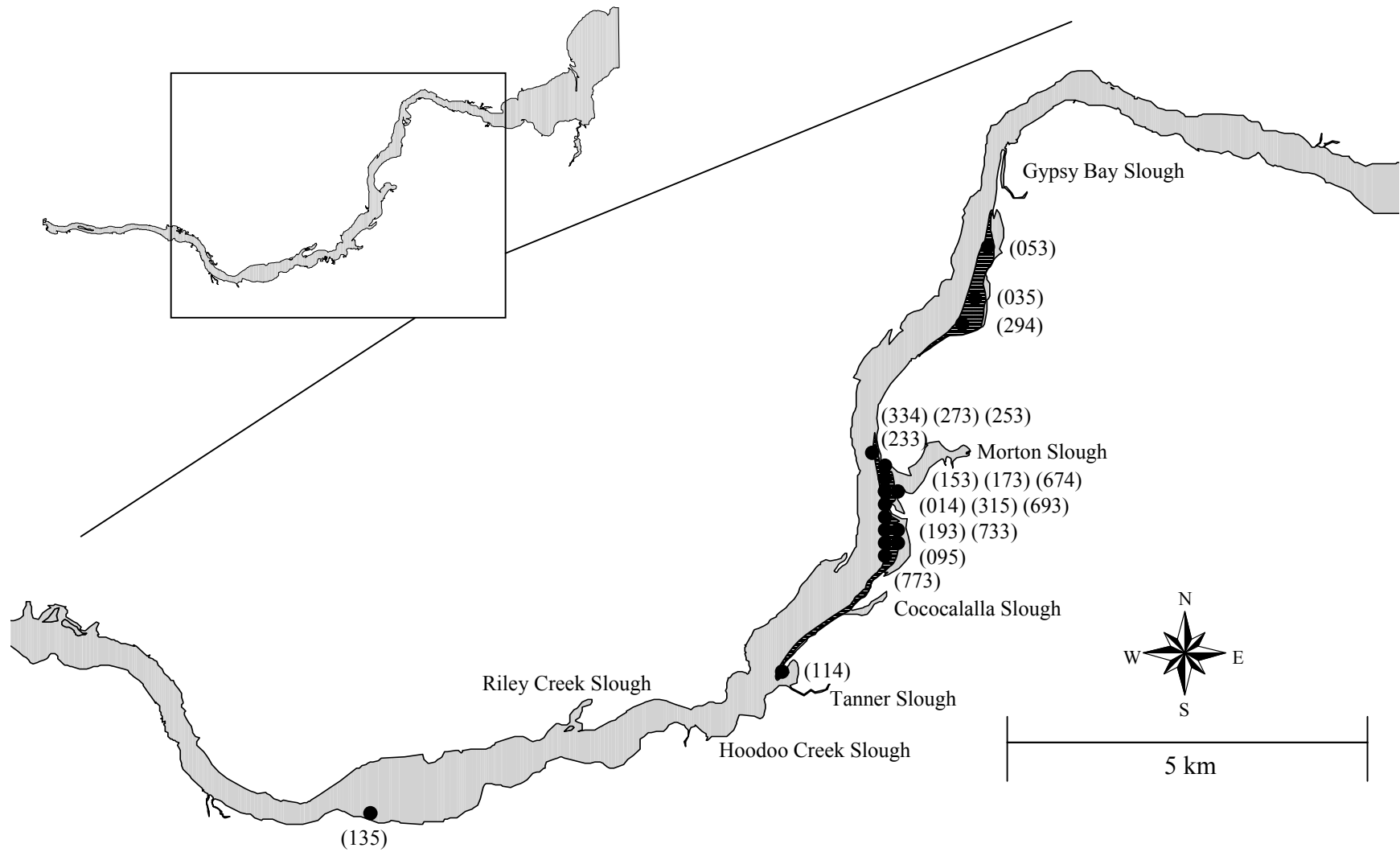


Figure 4. Locations of radio tagged largemouth bass in the Pend Oreille River, Idaho, on November 4, 2000 under 2.9 m winter drawdown conditions. Shaded areas indicate primary wintering areas (PWA) from November 1999 to March 2000.

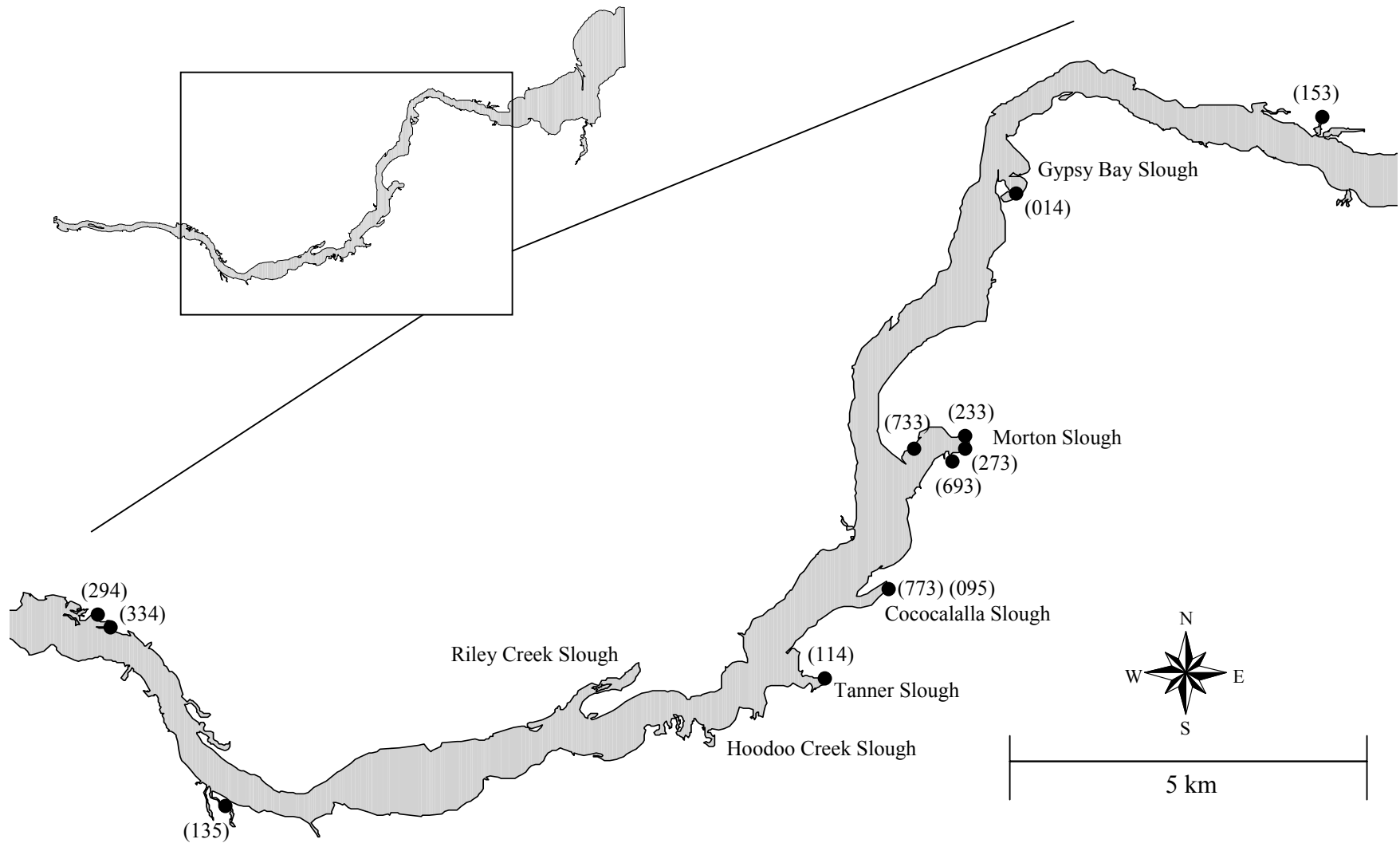


Figure 5. Locations of twelve radio tagged largemouth bass in the Pend Oreille River, Idaho, on 2 June, 2000.

Larval kokanee prey selection and growth

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Abstract: We investigated how springtime zooplankton community changes at Lake Pend Oreille, Idaho, have affected larval kokanee Oncorhynchus nerka (20-36 mm TL) by first conducting prey selection trials at three relative cladoceran to copepod prey densities, and at three levels of kokanee stomach fullness. We then compared growth rates of larval kokanee fed either cladoceran or copepod prey. In prey selection trials, random feeding occurred when cladocerans were scarce, but cladocerans were selected when their relative abundance increased. Stomach fullness affected the total number of prey items ingested, but not prey selection. Kokanee growth was not associated with prey selection, as the copepod diet produced the greater growth. These laboratory results suggest that species relative abundance rather than absolute abundance affects larval kokanee prey selection, and that growth is influenced more by total zooplankton densities than by densities of preferred prey items.

Introduction

The springtime crustacean zooplankton community at Lake Pend Oreille, Idaho has changed following introduction of the omnivorous freshwater shrimp Mysis relicta (Rieman and Falter 1981). Prior to mysis introductions, cladoceran zooplankton such as Daphnia spp. and Bosmina longirostris would be nearly undetectable by sampling throughout winter, then increase in abundance starting around April (Stross 1954). By June, cladocerans were abundant and utilized by kokanee Oncorhynchus nerka as food, with Bosmina accounting for the majority of prey items in immature kokanee stomachs (Platts 1958; Stross 1954). Currently, zooplankton grazing by mysis suppresses cladoceran populations until mid-summer, when thermal stratification of the lake excludes mysis from the warm epilimnion and releases cladocerans from mysis predation (Chipps 1997).

With cladoceran zooplankton unavailable as food for newly emerged kokanee, the copepods Cyclops bicuspidatus and Diaptomus ashlandi have become the principal prey items (Clarke 1999; Rieman and Bowler 1980). In a stomach contents analysis conducted in late May and June, 1998, Bosmina, which were present at densities ranging from 0.05 to $1.91 \cdot L^{-1}$, represented less than 1 % of the biomass ingested (Clarke 1999). A net pen study conducted in June in Lake Pend Oreille demonstrated that newly emerged kokanee can survive and grow on a diet consisting primarily of Cyclops, even when Cyclops densities were much lower than those historically found in the lake (Clarke 1999). However, the study did not estimate the effect of a diet switch from cladocerans to copepods on the growth of newly emerged kokanee.

Previous research on the growth of young planktivorous fish fed either cladoceran or copepod prey has yielded somewhat ambiguous results, with some studies finding no growth differences (Mayer and Wahl 1997) whereas others recorded faster fish growth on copepods (Confer and Lake 1987) or cladocerans (Mills et al. 1989). Differences in digestibility (Sutela and Huusko 2000) and caloric

values (Schindler et. al. 1971) between zooplankton prey could explain faster growth from a particular diet. Additionally, Stockwell et. al. (1999) showed that adult kokanee can reduce the water content of Daphnia during ingestion, thereby allowing for more prey biomass to be packed into the stomach. If kokanee larvae were similarly able to “squeeze” water from cladocerans, but not from copepods, then a cladoceran meal might provide a higher biomass, and potentially a higher energy content.

Few studies have addressed the importance of prey type on larval salmonid prey selection, perhaps because salmonid species hatch at a relatively large size and would not be gape-limited by zooplankton prey items. We are aware of no such studies published on larval kokanee. However, Confer and O’Bryan (1989) reported that prey selection of post-larval (32-50 mm total length) rainbow trout Oncorhynchus mykiss changed as prey densities fluctuate, with smaller food items selected more readily at high prey densities. They postulate that such selection preferences should lead to greater growth efficiency. In prey selection trials with other fishes, factors such as zooplankton taxa, density, and behavior, and the degree of gut fullness affected selection (Confer and O’Bryan 1989; Confer et. al. 1990; Drenner et. al. 1978; Johnston and Mathias 1994; Mayer and Wahl 1997; Visser 1982).

This laboratory study investigates how springtime zooplankton community changes at Lake Pend Oreille have affected larval kokanee by first testing the importance of relative densities of cladocerans and copepods to prey selection, and then comparing growth rates of larval kokanee fed either cladoceran or copepod prey. If a selection preference were clearly evident, then we hypothesize a priori that the preferred item will produce the greatest growth.

Methods

Overview

Our experiments were conducted using swim-up larval kokanee obtained from the Cabinet Gorge Hatchery (Cabinet Gorge, Idaho) and brought to the wet lab at the University of Idaho. Kokanee eggs at the hatchery are maintained in batches, with groups of larvae emerging approximately weekly from mid-February through April, enabling us to conduct multiple trials of our experiments in April and May, 2001 using recently-hatched larvae. Larvae were not fed while at the hatchery. Following transport from the hatchery, larvae were acclimated for 48 hrs, during which time they were fed a mixture of cladoceran and copepod zooplankton. In growth experiments, larvae were placed in holding containers and fed to satiation twice daily according to treatment group, with one group provided cultured cladoceran prey, and a second group receiving copepod prey strained from Lake Pend Oreille. Prey selection preferences were tested in a three by three factorial experiment, in which kokanee having three levels of gut fullness received one of three manipulated densities of cladoceran and copepod prey.

Ideally, cladocerans for the experiments would be Bosmina, the historically important early season food source for larval kokanee. However, culturing of Bosmina proved difficult, so we used the cladoceran Ceriodaphnia dubia. Ceriodaphnia cultures were maintained in 3.8 L plastic containers using filtered Lake Pend Oreille water, with daily feedings consisting of a mixture of digested trout chow, baker's yeast, and cultured Chlamydomonas algae. Copepods for these experiments were collected once weekly from the upper 5 m of Lake Pend Oreille using a 80 μ m mesh Wisconsin-style plankton net with a 20 cm diameter mouth, and held in plastic containers in filtered lake water. Typically, the zooplankton community in the lake from April through June consists largely of Cyclops

and Diaptomus (Clarke 1999), but we subsampled our zooplankton collections to verify taxonomic composition.

Growth Experiments

Growth experiments consisted of three replicate trials using 50 uniformly sized kokanee larvae (22-26 mm TL) that were selected for each trial. In each trial, 10-2 L flow-through cylindrical plastic containers, perforated at the mouth, were stocked with two kokanee each, and randomly assigned to either the Ceriodaphnia or copepod treatment group. Containers were kept partially submerged in a water bath maintained at 10° C (a typical Lake Pend Oreille surface water temperature in early June, personal observation) using a ½ hp in-line chiller unit with water pumped from the bath into each container. Dissolved oxygen was monitored periodically using a Yellow Springs Instruments dissolved oxygen probe. Lighting was provided for 12 hours each day using two 40-watt fluorescent bulbs. We estimated the mean beginning dry weight of experimental fish by drying the remaining 30 individuals to a constant weight in a 65° C oven, and weighing them to the nearest 0.0001 g.

Kokanee were fed for 1 h each morning (between 0800 and 1000 hrs) and evening (between 1700 and 1900 hrs) by shutting off the water flow, then introducing the prey. Field studies found a maximum of about 50 prey items in larval kokanee stomachs following evening feeding (Clarke 1999, unpublished data), so we assumed that stocking at least 200 prey items into each plastic container would more than satiate two fish. After 1 h, prey were removed from containers, and water flow was restored. At the conclusion of the experiments, fish were euthanized in MS-222, and fish weights (nearest 0.0001 g) were obtained after drying to a constant weight in a 65° C oven. Instantaneous growth rates ($G = \% \text{ change in body weight} \cdot \text{day}^{-1}$; Van Den Avyle 1993) were calculated for each fish. Growth rates were averaged for each container, and results from the three trials were pooled. An

ANOVA was used to test for significant differences between treatment groups (SAS Institute, Version 6.11). We also used Cohen's Effect Size ($d = (\mu_1 - \mu_2) / \sigma_e$; Cohen 1977) to assess the practical significance of our results based on differences among treatment means, where μ_1 and μ_2 are treatment means, and σ_e is the within groups population standard deviation from the ANOVA table. A d value of 0.2 denotes a small treatment effect, $d = 0.5$ is a medium effect, and $d > 0.8$ is a large effect.

Prey Selection Experiments

In prey selection trials, 6-2 L plastic containers were each stocked with one fish (22-36 mm TL) that had either an empty stomach, a full stomach, or a moderately full stomach. Fish having empty stomachs were starved for 24 hours, those with full stomachs were prefed to satiation with hatchery pellets 1 h prior to the experiment, while those having moderately full stomachs were prefed 3 hours prior. Each container then received live zooplankton, such that the number of zooplankton per liter in containers approximated either current springtime cladoceran to copepod ratios (2 cladocerans to 15 copepods $\cdot L^{-1}$), those found before Mysis establishment (15 cladocerans to 20 copepods $\cdot L^{-1}$), or an intermediate ratio (8 cladocerans to 17 copepods $\cdot L^{-1}$). Hereafter, we refer to cladoceran to copepod ratios as prey ratio 1 (2:15), prey ratio 2 (8:17), and prey ratio 3 (15:20). Zooplankton were amassed in preparation for feeding using plastic transfer pipettes to separate and count individuals into 2 g water-filled vials. We avoided a potentially confounding factor in which some larvae received mostly Cyclops copepods, while others received mostly Diaptomus, by selecting Diaptomus as the only copepod prey. In addition, we attempted to select only adult zooplankton as prey. Kokanee larvae were allowed to feed for 10 min, then were euthanized and preserved in 10% formalin. Each larvae was weighed (mg wet weight), the stomach was removed by dissection, and prey items were identified.

Chesson's modified selectivity coefficient (s), which is an appropriate estimate of prey selection when predation reduces densities of individual prey types, was calculated for each fish (Chesson 1983).

The coefficient is calculated as:

$$s_i = \frac{\ln((p_{i0} - r_i)/p_{i0})}{\sum_{j=1}^m \ln((p_{j0} - r_j)/p_{j0})}$$

where r_i is the proportion of items of food type i in the predators diet, and p_{i0} is the proportion of food type i present in the environment at the beginning of the foraging bout. In a two-prey type experiment such as ours, the index value for one prey type will be equal to 1 - the value for the other type.

Therefore, an ANOVA using copepod index values was used to investigate selection preferences.

Results

Growth

Four kokanee larvae died during growth experiments; three deaths occurred when fish escaped the holding containers through the water-flow perforations and were subsequently entrained in the chiller unit, while the fourth death was attributed to handling mortality. In each instance the container was maintained with one larvae thereafter. In designing this experiment, we were concerned that behavioral interactions between kokanee in individual containers might affect growth rates, thus we chose to use only two fish per container, and used as our treatment response the average growth per container. However, while observing fish activity during these experiments we saw surprisingly little interaction between individuals. Moreover, the coefficient of variation for ending kokanee weights (0.22) was similar to that for beginning weights (0.17), providing evidence that behavioral interactions between individuals in containers did not affect kokanee growth.

Kokanee fed copepod zooplankton grew faster than those fed Ceriodaphnia (Figure 1), although the difference was not statistically significant ($F=1.75$, $p=0.1964$). Cohen's Effect Size (d) was 0.10, indicating a small treatment effect. Instantaneous growth for larvae fed copepods averaged $1.61\% \cdot \text{day}^{-1}$ (range = -0.85 to $4.39\% \cdot \text{day}^{-1}$), while those fed cladocerans averaged $0.92\% \cdot \text{day}^{-1}$ (range = -0.62 to $2.39\% \cdot \text{day}^{-1}$). Zooplankton strained from Lake Pend Oreille, and fed to kokanee in the copepod treatment group, consisted entirely of copepods, with the majority (83%) being Cyclops.

Prey Selection

We found that selection was significantly influenced by prey ratio ($F=3.32$, $p=0.0374$; Figure 2). However, gut fullness alone did not significantly influence prey selection ($F=0.59$, $p=0.5573$), and no statistically significant interaction existed between gut fullness level and the ratio of cladocerans to copepods ($F=1.05$, $p=0.3829$). At the lowest Ceriodaphnia to Diaptomus ratio (prey ratio 1), kokanee selected Diaptomus ($s=0.54$) slightly more than would be expected from random feeding ($s=0.5$), but when Ceriodaphnia increased relative to Diaptomus, then Diaptomus selectivity coefficients declined to 0.44 for both prey ratios 2 and 3. No relationship existed between the size of larvae (range= 0.036 - 0.40 mg) and selectivity index values ($r=0.10$, $p=0.2038$).

The total number of prey items ingested by kokanee increased significantly as zooplankton ratios increased ($F=16.86$, $p<0.0001$; Figure 3), and as stomach fullness increased ($F=21.38$, $p<0.0001$). The mean number of zooplankton ingested nearly doubled from prey ratio 1 (10.25 items/stomach) to prey ratio 3 (20.28 items/stomach), and declined by nearly half from an empty stomach (21.16 items/stomach) to a full stomach (11.95 items/stomach).

Discussion

Field studies have shown cladoceran zooplankton to be an important component in the diet of larval kokanee (Stross 1954; Northcote and Lorz 1966; Foerster 1968; Burgner 1991). In some instances kokanee larvae have actively selected cladocerans (Beattie and Clancy 1991), whereas in other instances they have not (Clarke 1999). Therefore, the effect of varied prey assemblages to larval kokanee prey selection is not well understood, and the effect of prey type on growth has been untested.

In these laboratory experiments, the relative density of cladoceran to copepod prey clearly affected feeding selection by larval kokanee, but no growth benefits were evident from feeding on the preferred prey, causing us to reject our a priori hypothesis that the preferred prey would produce the greatest growth. Our prey selection trials can be summarized as follows: Kokanee fed nearly randomly when Diaptomus were disproportionately abundant (i.e. prey ratio 1), but fed selectively on Ceriodaphnia when densities increased relative to Diaptomus. These laboratory results provide perspective for understanding a prey selection study of wild larval kokanee in Lake Pend Oreille that found little preferential feeding despite estimated cladoceran densities ($3 \cdot L^{-1}$) that appeared unusually high compared with prior year estimates (Clarke 1999). In that study, copepod density estimates were usually greater than $30 \cdot L^{-1}$, making cladocerans scarce relative to copepods. Therefore, results from these laboratory experiments are congruent with our field observations, and support a conclusion that relative prey densities are an important determinant in larval kokanee prey selection. In prey selection experiments with three-spined stickleback Gasterosteus aculeatus, relative abundance of the preferred prey type was found to be more important to prey selection than absolute abundance of any prey item (Visser 1982).

We did not attempt to relate larval kokanee prey selection to fluctuating total prey densities. Optimal foraging theory predicts that predators will feed more selectively as total food densities

increase, yet some evidence suggests that the theory may not apply to larval fishes. Juvenile larval walleye Stizostedion vitreum (>20mm TL) did not feed more selectively when prey densities increased by more than an order of magnitude (Mayer and Wahl 1997), and selection of preferred prey by young yellow perch Perca flavescens (22-62 mm TL) did not increase with increasing food densities (Confer et al. 1990). Furthermore, the diets of young fish in some feeding studies broadened to include less preferred prey types when prey densities increased (Johnston and Mathias 1994; Mills et al. 1987), a phenomenon referred to as “negative switching”. Therefore, while we cannot rule out the possibility that increased total zooplankton densities, rather than changes in relative Ceriodaphnia densities, were responsible for the results we observed, there is ample evidence to support the latter conclusion.

As expected, the average total number of zooplankton ingested by kokanee larvae decreased as stomach fullness increased, but we saw no influence of stomach fullness on prey selection. Because Ceriodaphnia is generally considered to be an easily captured zooplankter (Drenner et. al. 1978), we anticipated that it would be strongly selected by satiated kokanee. Other studies have found strong correlates between selectivity and satiation (Bence and Murdoch 1986). However, it appears that prey size rather than evasiveness is the important determinant for prey selection by satiated fish, with smaller prey being preferred. Reported length estimates for Ceriodaphnia range from approximately 0.30-0.70 mm (Culver et al. 1985; McCauley 1984), while Diaptomus averages about 0.69 mm in June in Lake Pend Oreille (Clarke 1999). Therefore, we suspect that prey in our experiments were too similar in size for selection preferences by satiated fish to occur. As a result, we may still not fully understand the importance of Bosmina, the smallest of crustacean zooplankton, in the diet of nearly satiated wild fish.

Our growth results refute suppositions that cladoceran zooplankton provide an inherently better meal for larval kokanee than do copepods. Growth during these experiments was slightly faster from

fish fed copepods, a result that could be explained by differences in caloric values. In the literature, caloric values for copepods are generally about 10% higher than those of cladocerans (Comita and Schindler 1963; Schindler et al. 1971). Cultured zooplankton are grown in a food-rich environment, and should have higher than normal caloric values (Confer and Lake 1987), so any bias from using lake-caught versus laboratory-reared zooplankton should have favored the Ceriodaphnia fed fish.

If a copepod diet provides better growth, why would kokanee select Ceriodaphnia in these experiments? Two potential explanations appear plausible. First, Ceriodaphnia may have been the more visible of the two prey types, possibly due to its eye pigmentation or presence of eggs, both of which would result in greater contrast for an otherwise relatively transparent organism. Studies have demonstrated that planktivorous fish feed selectively on cladocerans with more prominent eye pigments (Zaret and Kerfoot 1975), and on those with eggs (Mellors 1975), highlighting the importance of contrast to visual predators. Furthermore, Ceriodaphnia possesses a rounded body form that could increase its visibility to laterally searching predators. In a shallow water environment such as our experimental containers, lateral searches by kokanee would be the norm. Second, studies show that when detected, cladoceran zooplankton are more easily captured than copepods (Confer and Blades 1975).

Clarke and Bennett (in press) theorized that total zooplankton densities were more important than zooplankton species composition for predicting larval kokanee survival and growth. These laboratory studies support that hypothesis. For that reason, we believe that efforts to correlate larval kokanee cohort mortality with food abundance should focus on total zooplankton densities or biomass, rather than cladoceran densities or biomass.

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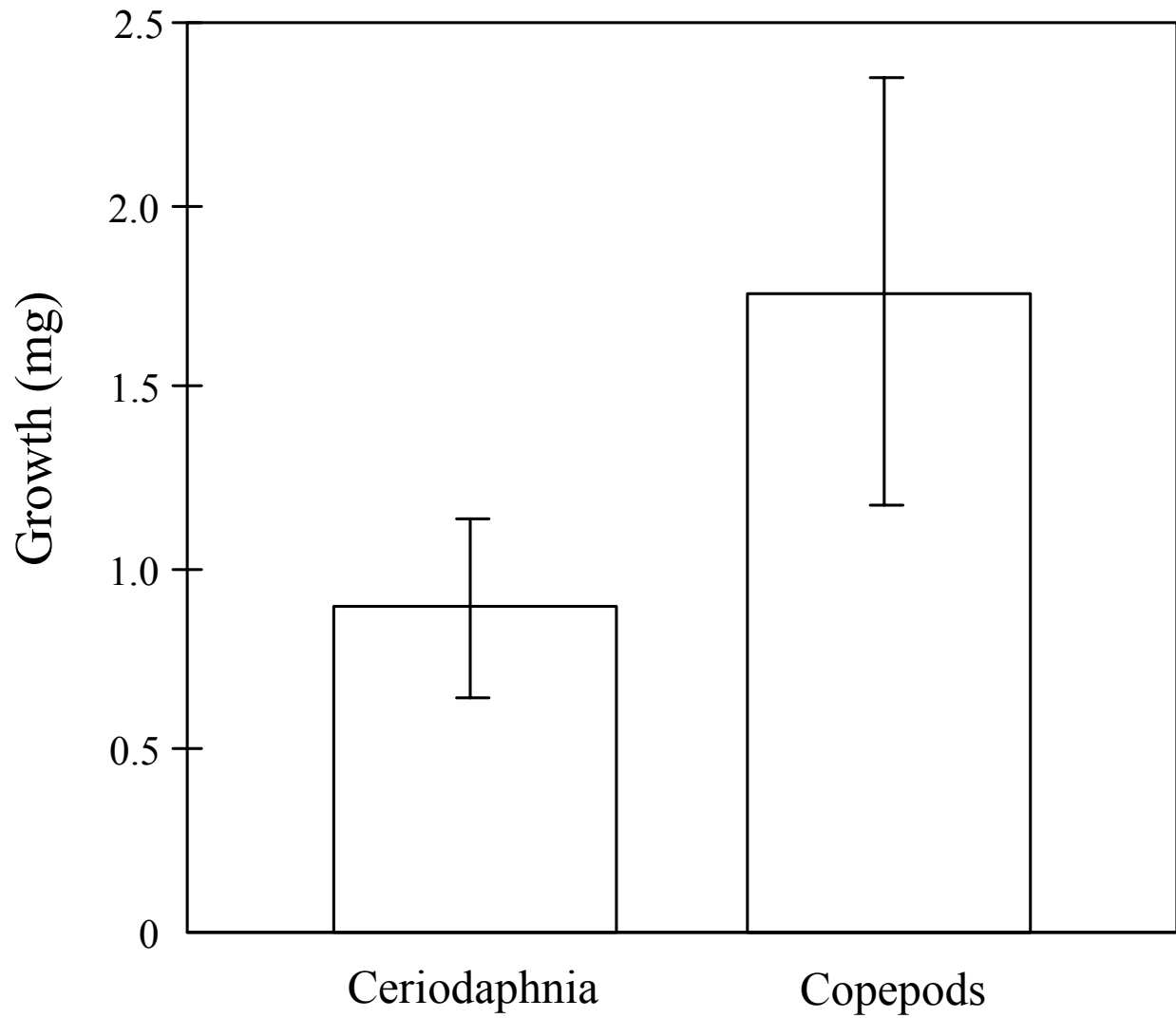


Figure 1. Mean kokanee growth (ending weight - beginning weight) fed either Ceriodaphnia or a mixed copepod diet for ten days. Vertical lines represent one standard error.

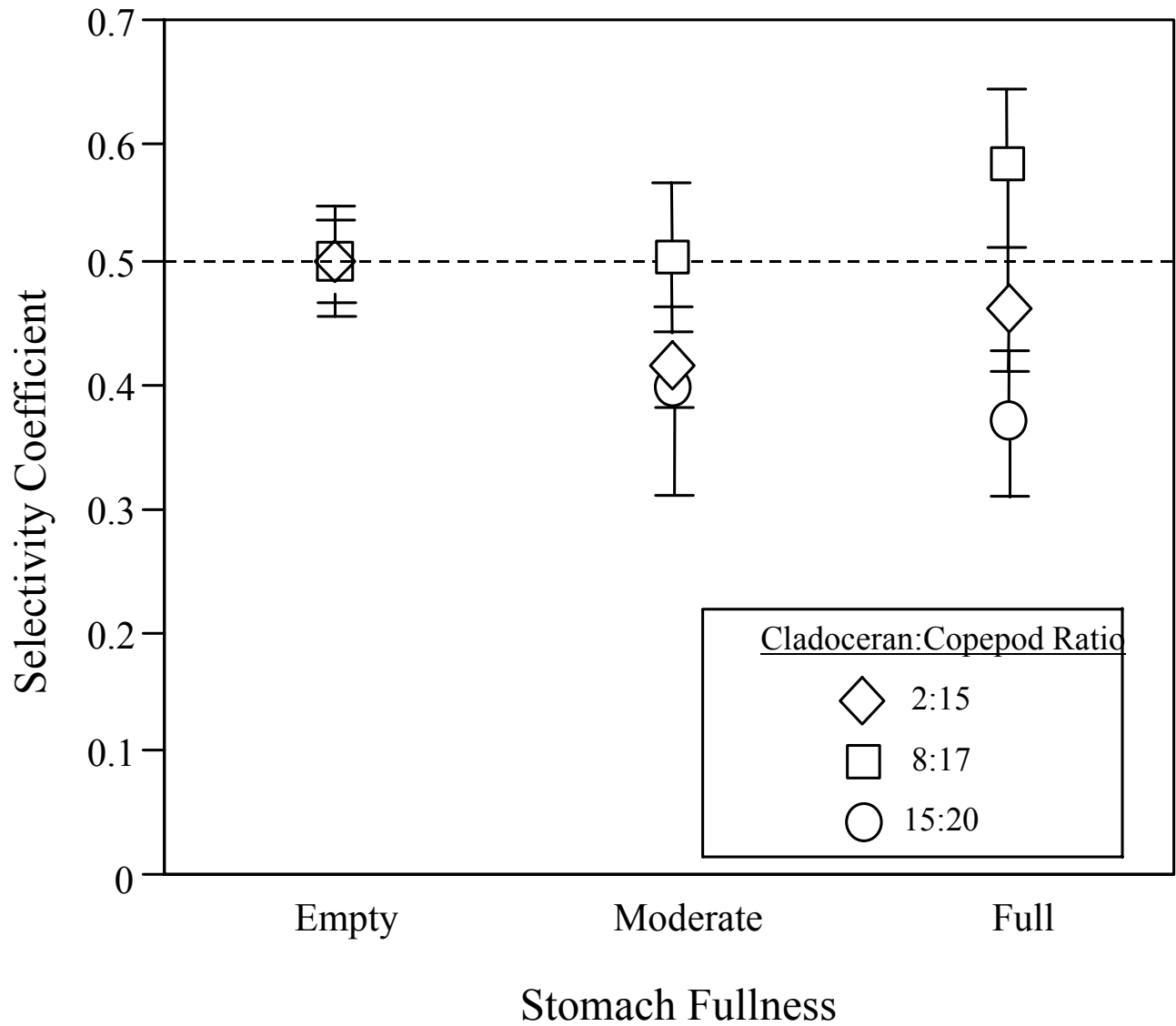


Figure 2. Chesson's selectivity coefficient (α) for kokanee feeding on *Diaptomus* at one of three relative prey ratios, and at three levels of gut fullness. Dashed line represents random feeding, vertical lines represent one standard error.

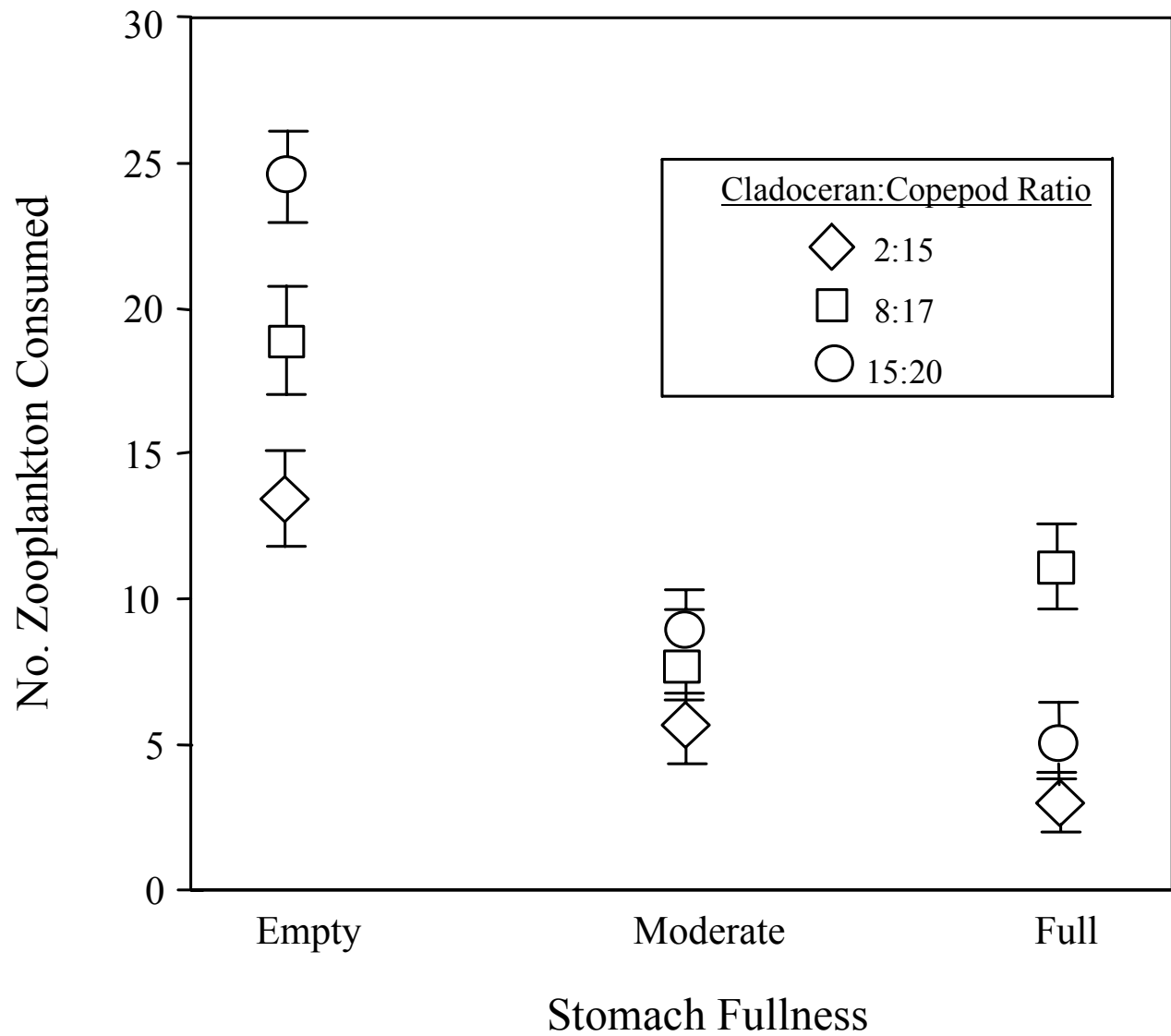


Figure 3. Mean total number of prey items ingested by kokanee feeding at one of three relative prey ratios, and at three levels of gut fullness. Vertical bars represent one standard error.